THE THEORY OF SEX AND SEXUAL GENESIS.

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IN sexual genesis the germinal aggregate with which the development of the new individual begins is the product of the union of two generative cells. One of the combining cells—the female element, or germ-cell—is a very large one; while the other—the male element, or sperm-cell—is a very small one. Their union is effected by the sperm-cell, or its generative matter, penetrating into the body of the germ-cell; and the former loses its identity and integrity as a cell in the act of union, while the latter does not. Sexual genesis, in its initial stage, is thus a dual process, consisting in the coöperation or combined action of two factors, and these factors are comprised in the contents of generative cells that are morphologically distinct.

The fundamental problem in the theory of sexual genesis, with regard to the physiology of the process, is this: Are the two factors of the process represented in these two classes of morphologically distinct generative cells likewise functionally distinct, and complementary the one of the other? And, if so, What are the physiological differences between them, and what the need and rationale of their observed mode of coöperation in the generative process?

Besides explaining the physiological differences and relations to each other of the male and female generative elements, an adequate theory of sex and sexual genesis must also explain the correlated morphological and functional differences between male and female organs or organisms.

The Advantage of Genesis by Germ-cells.—The development of an individual organism may begin with the contents of a single generative cell, which may or may not be the product of the union of two cells, or it may begin with a bud or gemma composed either of an aggregate of untransformed cells or of portions of partially differentiated tissues. Leaving out of consideration for the present the fact that in sexual genesis the original contents of the germ-cell requires impregnation by a sperm-cell in order to enter upon the normal developmental changes, I wish here to point out that the former mode of the origin of new individuals gives an important advantage in the perpetuation of species, so far as perpetuation depends on the production of a great number of off-

spring. The explanation of this advantage may be given as follows: In order that a germinal aggregate may develop into a distinct individual, with a due coördination of its parts about a distinct axis or center, the formative conditions within it must first be, in some manner and to a great extent, isolated from the formative conditions in the parts of the parent-body in connection with which its production as an aggregate has taken place; otherwise its unity of development as a distinct individual would be interfered with, or we may say would be impossible. For this reason the size which a bud is required to have in order to enter upon an individual development is much greater than the size which a germ-cell is required to have. This follows from the manner in which a bud is formed. In the simplest case for multicellular organisms, a bud is formed by the outgrowth by cell-multiplication of an aggregate of cells from a layer of undifferentiated cells of the parent body. Thus in the first stages in the growth of the bud, both the cells which compose it and the cells of the layer from which it is produced, must be in a plastic, formative state in order that the growth of the bud in this manner may go on. And the isolation that is requisite to its distinct individual development is only brought about by sheer outward growth away from the producing cell-layer. That is, the bud must necessarily, from the mode of its formation, attain considerable dimensions before its independent development can begin.

On the other hand, where the development begins with the contents of a single germ-cell, the requisite isolation of the formative conditions within it is brought about, not by growth in size, but by the germinal mass becoming inclosed by a distinctly differentiated cell-wall, or capsule, or embryo-sac. And thus, as in the higher plants, we find that the first stages in the development may take place with the new individual completely inclosed on all sides with tissues of the producing organism in which vital processes are actively going on. This surrounding tissue itself forms a small bud, but one of low organization and generally much smaller than any bud that is fitted for functions of self-maintenance. The eggs of animals in like manner become isolated in their formation, but are discharged from the producing organ before their development begins.

In consequence of these relations an immensely greater number of seeds or eggs fitted for a complex development can be

produced by a plant or animal than of bulblets or gemmæ. Moreover, when produced they are better adapted for dispersal, in the case of seeds, to suitable situations for their growth; and in the case of eggs, may be deposited in favorable situations by the producing animal.

This advantage of genesis by germ-cells over genesis by the production of buds, obtains in all the lower grades of organisms in which the perpetuation of species depends, to a great extent, on the production of a large number of offspring. For the higher animals, or for all terrestrial animals, there is the further consideration that the large buds which they would have to produce, and the mode in which they would have to produce them in order to keep up the succession in this way, would so encumber the producing organism as greatly to lessen its powers of self-conservation. As a matter of fact we do not find any terrestrial animal reproducing by buds. The highest aquatic animals that do so are the Tunicata or Ascidians. In these the buds are produced from a large stolon, which the medium in which the animal, or associated group of animals, is supported, enables it to carry with it without any great interference with its self-conservative actions. Besides, in the aquatic mode of life the whole body may be soft, and that high degree of differentiation of the tissues is not required, at least in all cases, that is required in terrestrial animals. But all animals and plants, except the lowest, that reproduce by the formation of buds, also reproduce from germ-cells. In such cases, to whatever advantages the former mode of genesis has in keeping up the succession, is added the advantage, here pointed out, which attends the latter mode.

The Rationale of Sexual Genesis.—Admitting that there is an advantage, of the kind above explained, attending genesis by germ-cells, in the perpetuation of species, the further question arises, of what the advantage or need is of the addition to the original contents of the germ-cell of the matter of a sperm-cell, in order that the single mass may be fitted to initiate the development of a new individual. No doubt a considerable advantage results from crossing. But crossing does not always take place in sexual genesis. Besides, to assign this reason is not to give a fundamental explanation. It leaves the physiological difference between the two kinds of generative cells to be determined, and the requirements of the formative and developmental processes to be assigned which makes this difference necessary.

The germ-cell and the sperm-cell cannot be regarded as physiological or generative equivalents—leaving out of the account for the present their morphological characters. They are physiologically differentiated, though not specialized in the sense in which the component cells of the various tissues are specialized. It is the function of the cells of each of the different kinds of tissues, as specialized cells, to form or secrete from substances derived from the general plasma of the organism, some organic compound of specific constitution, which is either deposited in contact with the protoplasm of the cell as a solid or semi-solid component part of the structure of the tissue, or is thrown out as a liquid secretion by the bursting of the cell-wall. The functions of the two kinds of generative cells are not such that their differentiation from each other could be of a nature to render them specialized in this sense. But since the office of sexual genesis consists in the production of organisms as wholes, and not merely of limited parts of organisms, we may fairly infer that in so far as the developmental process in general can be analyzed into two essential factors, it is these two factors which constitute the organic basis of the dual character of the function of sexual genesis, and therefore that it is with reference to these two factors of the process that the two kinds of generative cells have been differentiated, and not with reference to special products of the process. Two such general factors are commonly distinguished by biologists as comprised in and making up the whole process of development, namely, growth and differentiation; or, since cell-division is the basis of differentiation, we may say that in the more strictly formative stage in the development of any organ or tissue, the two factors are cell-growth and cell-division. Hence the presumption on general grounds is, that one kind of generative cells represents one of these factors, or results from differentiation in the direction of one of these factors, and the other kind represents the other factor.

The facts sustained this presumption, and at once indicate to which kind of generative cells each factor in an excessive degree belongs.

Germ-cells attain a greater size than any other formative cells. Says Professor Minot: "It is a rule, no exception to which, I believe, is known, that the mature egg-cell is much larger than any other cells in the body of the parent" (AM. NATURALIST, Feb.,

1880). On the other hand, sperm-cells are among the smallest cells of the producing organism. Mature germ-cells result from the extraordinary growth without division, of certain of the primitive germinal cells of the ovary, generally with the aid of the formative activity of other smaller cells by which they are surrounded. In animals "the spermatozoa are formed by the breaking up of the male germinal cells, or of cells secondarily derived from them by division. The cells which directly give rise by division to the spermatozoa may be called spermospores, and are equivalent to the ova or oöspores" (Balfour, Comp. Embryol., Vol. I, p. 53). Pollen-grains in like manner are produced by the subdivision of a mother-cell. In all except "the lowest forms of vegetable life * * * the two cells that take part in the act of sexual union * * * are strikingly different in size, form and physical properties. In these cases one of the two cells, the male cell, conveys to the other only a small quantity of material by means of which it produces an effect upon it; this other cell, the female cell, contains by far the largest proportion of the material which takes part in the development incited by the act of union" (Sachs, Botany, p. 224).

Thus in the production of germ-cells there is evidently a relative preponderance of the factor of growth; and in the production of sperm-cells there is a relative preponderance of that factor of the developmental process which is more especially concerned in cell division.

We have next to inquire why this relation or differentiation between the two kinds of cells should be necessary to their coöperation in the initiation of a complex development.

A germinal aggregate which is fitted to initiate the development of a complex organism must be an aggregate of considerable size, in order that it may afford an adequate basis for the incipient formation of the different parts. The production of such an aggregate can only take place on condition of the absence of a tendency in it to undergo segmentation, and thus enter upon developmental changes while it is yet small. It must be so constituted and so placed that there is a relative deficiency of the factor of cell-division in the formative processes by which it is produced. Then, when it has attained the requisite size, it is still unfitted for active development until this deficiency is supplied, and the proper balance between the two factors is restored.

This result is brought about by the accession to it of a sperm-cell, which represents a relative preponderance of the factor of cell-division, and the development is then begun with that degree of energy which is necessary to insure its going on to completion. In every species of organisms a certain mean adjustment of these two factors to each other is suitable to the formation of organs and tissues having the requisite structural characters, after the first stages of the development have been passed through. In the germ-cell there is a departure from this mean standard of adjustment in one direction, and in the sperm-cell a departure in the opposite direction; the departure in the one case being necessary to the formation of a single aggregate of sufficient size to serve as the basis of the development, and the departure in the other case being necessary to the formation of germinal matter fitted to restore the balance by its union with the larger aggregate. This I believe to be the fundamental principle in the theory of sexual genesis.

But in parthenogenesis the germ-cell undergoes development without impregnation by a sperm-cell; and at first it may appear that the theoretical conclusion here arrived at is irreconcilable with this fact. It may be shown, however, that it is not. In the first place, parthenogenetic eggs or germ-cells are generally smaller than eggs that require fertilization. In the second place, whether they are smaller or not, the individuals developed from them do not generally if ever attain to as high a grade of organization as those developed from impregnated germ-cells. So conspicuously is this the case in plants, that Sachs bases his interpretation of the phenomena and advantage of sexual genesis on this observed difference. In the third place, the normal balance between the two factors of the developmental process may be restored in the germ cell, but not so completely, in other ways besides impregnation by a sperm-cell. This may result from a freer access of oxygen to it after it has been discharged from the producing organ; by its absorption of water, with other matters in solution, which have a tendency to set up active changes within it; or by its being subjected to a higher temperature than that at which it was kept during its formation. By one or another or all of these changes of conditions the balance may be sufficiently restored to cause the development to go on; but not so completely restored as it is by the accession to the germ-cell of a

sperm-cell, in addition to changes in some of the external conditions here mentioned. And in sexual genesis there is the further difference that whatever advantage there is in crossing, or in the union of two portions of germinal matter derived from different sources, is also secured.

The Redundant Sexual Type.—In the early stages of embryonic development in the higher animals no distinction as to sex is apparent even in the sexual organs. Having regard to this fact, the view which had come to be generally accepted among physiologists, before the advent of Darwin's theory, with respect to the morphology of the sexes, was, that there is a common type for all the individuals of both sexes in a species. But by most physiologists this type was not believed to be hermaphroditic. "The early type of the sexual organs is to be regarded as common and single rather than double, as some have considered it" (Allen Thomson, Todd's Cyclop., Vol. II, 1839, Art. Generation). In the article on hermaphroditism in the same work, Simpson adpots, as he says, "the opinion commonly received by physiologists of the fundamental unity of sex among all individuals belonging to the higher animals; or, to express it otherwise, we have assumed that each individual is, when normally formed originally furnished with elemental parts capable of forming one set of sexual organs only." Still he refers to the rudimentary sexual organs in each sex as analogues of developed organs in the opposite sex. The most familiar and striking examples we have of such rudiments are the rudimentary mammæ in male mammals and the clitoris in females.

When Darwin adduced the existence of rudimentary organs as evidence in support of the theory of descent, and as facts that are inexplicable on any other theory, he made no distinction between rudimentary sexual organs and rudiments of organs that pertain to individual self-maintenance. The only possible or reasonable explanation of the existence of the latter is that they are reduced representatives of organs that were functional in the ancestors, in some former period, of the organisms of the present time in which they are found. And the same explanation was applied by Darwin to the rudimentary sexual organs—which explanation has generally been adopted by his followers. But against this explanation in the case of the sexual rudiments two valid objections may, I think, be made. In the first place, none of the

highest animals of the present time are functional hermaphrodites. Says Gegenbaur: "The hermaphrodite stage is the lower, and the condition of distinct sexes has been derived from it. This change is due to the decrease in size of one or the other organ, so that hermaphroditism is the precursor of sexual differentiation. This differentiation, by the reduction of one kind of sexual apparatus, takes place at very different stages in the development of the organism, and often when the sexual organs have attained a very high degree of differentiation. In these cases ontogeny exhibits the two kinds of organs primitively united, and so causes the individual to be hermaphrodite at a certain stage in development" (Compar. Anat., Eng. ed., 1878, p. 54). But this general hypothesis becomes inconsistent with the facts when carried out in its application to the higher vertebrate animals. It is in the highest animals that the most perfectly formed rudiments are found, in each sex, of the sexual organs that in their developed or functional state are proper to the opposite sex alone. If they are reduced representatives of organs that were once functional, those organs must have been functional in animals of the same grade and type as those in which the rudiments are now found; otherwise the rudiments would not be the exact analogues or reduced representatives which they are, of the functional organs at the present time of the opposite sex. And no physiological reason can be assigned why animals in other respects of the same type and grade of organization, which are best fitted to perpetuate their species by a complete functional differentiation of the sexes, at the present time, should have been better fitted to do so as hermaphrodites at a former period. In the second place, the whole morphological type of the reproductive organs of either sex in any species of the higher animals, comprising both rudimentary and developed sexual organs, does not make up a full complement of the developed sexual organs of both sexes. Referring to the higher animals, Simpson says: "An hermaphrodite was defined by the ancients as an individual capable of fulfilling by turns the reproductive functions of both sexes, or at least one who simultaneously possessed both the male and female organs fully developed; such a being, however, is not only unknown among the authentic details of anomalies, but is physically impossible in man and the higher orders of animals without extensive alterations in the connections of the bones and

other parts of the pelvis. "The type of development [from common embryonic parts] of the genital organs may be stated to differ in the different parts of the system in the two sexes as follows:

"1st. It is single and homological in the external organs.

"2d. It is double and heterological in the middle organs or passages.

"3d. It is partially double and heterological in the productive organs" (Quain's Anatomy, 1876, Vol. II, p. 814).

The morphological sexual type of either sex comes thus short of comprising a complement of the developed organs of both sexes, owing to the fact that for some of the organs, or parts of the sexual apparatus, the same primary tissue develops into a male organ or part, in one sex, and into a female organ or part in the other sex. But the common fundamental type of the species is redundant as to the number of organs required to be developed in either sex alone, owing to the fact that for some of the organs the same primary tissue that is required for functional parts, in one sex, cannot be converted into functional parts in the other sex. In the higher animals, therefore, the normal development of each male or female individual is a one-sided development of this sexually redundant type, and not a one-sided development of an embryonic hermaphrodite.

Thus much premised, two questions of theory have to be answered in order to make all the phenomena of sexual development intelligible. We wish to know why it is that useless rudiments appear in one sex of organs that are only required to be functional in the other sex; and we wish to know how it is that, except in rare cases, each individual, presenting at first the common embryonic type of the whole species, afterward undergoes complete development in the adult sexual characters of one sex or of the other sex alone, and does not take an intermediate course of development between the two adult types.

1. In order that a germ-cell and a sperm-cell may effectively unite in the initiation of the development of a new individual, there must be an approximately complete correspondence between the two as complementary factors of the single course of evolution. There are two conceivable ways in which individual organisms might be produced having the necessary sexual organs of either sex alone fully developed, without rudiments of those that are functionally proper to the other sex being formed. One way

would be for each female parent organism to produce two kinds of ova or germ-cells, one kind fitted to initiate the development of male, and the other the development of female offspring, while each male parent organism produced two corresponding kinds of sperm-cells. The other way would be for only one kind of ova and one kind of sperm-cells to be produced in a species, but for each embryo to be deflected to a one-sided development—that of one of the sexes—so early and so completely that no perceptible rudiments of the sexual organs proper to the opposite sex should at any time be formed. The first method is evidently too complicated ever to be established and maintained in any species by natural selection, at least without some great advantage in the perpetuation of the species could be gained by it that could not be secured in any other way. The second method is actually exemplified in a great many of the lower monosexual organisms, where the requisite sexual organs consist simply of an ovary or pistil in the one sex and a testicle or anther in the other. In these no persistent rudiments of the organs of the opposite sex are perceptible in individuals of either sex. But in the higner animals, where a complicated apparatus in intimate correlation with the other parts of the body is required in each sex for the performance of its part of the reproductive function, so early and complete a deflection of the course of development, with respect to these organs, cannot take place. A certain set of sexual organs of the sexually redundant type must be developed to a functional state in each sex; and the intimate structural connection and functional coördination with the other parts of the body demanded in the efficient performance of their functions, makes it necessary that their development be initiated at an early stage in the development of the embryo. But an organism of great complexity can be evolved only on condition that the parts of the embryo shall not become highly differentiated in the early stages of the evolution—on condition that the various parts of the forming body retain for a considerable time their plasticity. In its early stages, therefore, the embryo, considered as a conditioning apparatus of its own formative processes, is necessarily unfitted to have established, or maintained within it, so sharp a differentiation of the conditions of those processes, as affecting the development of the sexual organs, as would be necessary to cause those organs that are functional in either one of the sexes only to enter upon a complete development, and at the same

time cause the development of the organs that are redundant to that sex to be so completely arrested that not even rudiments of them should appear. This explanation agrees with and also explains a law of variation enunciated by Darwin, namely, that "variations which appear early in life in either sex, tend to be developed in both sexes" ("Descent of Man," p. 232).

The existence of rudimentary sexual organs is thus, I think, satisfactorily accounted for, without assuming that they represent organs that were once functional in the sex in which they are found. In the course of descent of a species it is the common type of the species—which is redundant as regards the organs that are required to be functional in either one of the sexes—that undergoes modification by adaptive variation, and by the natural selection of irrelative variations through the succession of the best reproducers. Those organs of the redundant type that are functionally proper to either one of the sexes have their characters determined by natural selection acting within that sex. But if, owing to the conditions above explained, a developed organ in one sex is represented by a rudiment in the opposite sex, any modification of this part of the common type will not only appear in the developed organ of the one sex, but also and correspondingly in its rudiment in the opposite sex. Thus, for the higher animals at least, the rudimentary sexual organs are to be regarded as having been acquired *as rudiments* in the sex in which they are found, and not as representing organs that were once functional in that sex. This explanation accords with the fact that such rudiments are most perfectly formed in the highest animals, where the developed sexual organs themselves attain the highest degree of organization as specialized parts.

No doubt there are cases among plants in which the reproductive individuals, or members of a composite individual, are now unisexual, and possibly among the lower animals also, where rudimentary sexual organs do represent organs that were functional at a former period, when the species was hermaphrodite. But in many cases it would be difficult to determine whether the actual course of modification by which the present reproductive type of the species has been reached, has been by the reduction of organs that were once functional to a rudimentary state, or by the acquisition of the rudiments as parts of the common reproductive type of the species.

(To be continued.)